THE FRUITS AND SEED PRODUCTIVITY IN *XANTHORRHOEA*

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(Plates XIII and XIV)

Synopsis

A study of the productivity of the tricarpellary fruits in species of *Xanthorrhoea* was made. Seed counts of a total of 3,992 fruits of *Xanthorrhoea resinosa*, *X. australis* and *X. preissii* showed an overall average of 2·1 per fruit. Notice was taken of fruit productivity in relation to linear position on the inflorescence axis and it was apparent that seed productivity was lowest at each end of the inflorescences. As flowers open late in these positions, ovule abortion is thus higher in late opening flowers. Seed output was well below the possible maximum that could be produced by flowers reaching anthesis—only 0·1 to 5·2 per cent—and even these figures are greater than total ovule abortion by more than 50 per cent when the loss before anthesis of six to seven out of eleven flower primordia in each floral cluster is considered.

The production of more than one seed per loculus occurred in 24·5 per cent of fruits counted, but fruits with one set of twins accounted for 18·5 per cent of this figure. Maximum seed number per fruit was seven while the greatest number of seeds found in one loculus was four. Speculations concerning greater seed output in a single season by shaded, arborescent plants than by more frequently flowering non-arborescent plants were made. Factors such as arborescence, high food storage capacity and shading could contribute to the production of more polymorphic seeds. High abortion rates of seeds in plants growing in open habitats may be increased by water stresses in drier habitats. The mechanism of staggered times of anthesis in combination with production of excessive numbers of flower primordia and high ovular abortions provides a dynamically fluid strategy that could overcome problems such as intermittent water stresses and insect predations with ease.

INTRODUCTION

Over a period of several years, the author has been interested in various aspects of the biology of the Australian grass tree *Xanthorrhoea* (Staff 1968, 1970, 1974, 1975). Although most interest has centred on the anatomy of the plant, data have been collected from time to time on the seed productivity of fruits of some of the plants.

Salisbury (1942) presents detailed records of fruit and seed counts of large numbers of British plants and makes the generalisation that plants growing in intermittently open habitats produce most seeds. Next in productivity are those that grow in permanently open, semi-open and closed unshaded habitats, which, in turn, produce more seeds than those growing in shaded communities. However, comparison between these groups was rendered difficult by the presence of large numbers of annuals in the first three community types and by the preponderance of perennials in the closed communities. Harper and White (1974) have reviewed much of the pertinent literature on reproductive output of perennials, including a treatment of the great fluctuations that can occur in seed output by such plants from year to year and of fluctuations resulting from differences in age and vigour of the plant. It is difficult to generalise about seed productivity of perennial monocotyledons, however, as wide ranges have already been recorded. Schwerzel (1967) has shown a mean seed number of 40 per plant for *Cyperus rotundus* and 820 for *C. esculentus* in one season. In the orchids, seed productivity is much greater—Salisbury (1942) recorded an average output of 56,000 seeds per plant, for *Orchis maculata*. This figure has been exceeded by

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Darwin (1882) who recorded 1,756,440 seeds in a single capsule of *Maxillaria* sp, and as these plants often produce six capsules, a seasonal total of the order of ten million seeds would result.   Hager (1952) found 929,000 viable seeds in a single capsule of a *Cattleya labiata* hybrid which had a total seed production of between two and three million seeds.   These plants are all relatively small in size compared to the arborescent monocotyledons, which also have a wide but not as great a range of seed productivity.   Annual productivity of 300 plants of the polycarpic *Cocos nucifera* (the coconut palm) (Manthriratna, 1973) was between 50 and 100 seeds.   Ellis (1913) found a range of 20 to 719 perfect seeds per plant in *Yucca glauca*, while Tomlinson and Soderholm (1975) found an estimated 250,000 seeds in the inflorescence of the monocarpic palm *Corypha elata*.

Waterhouse (1967) describes the tricarpellary fruits of *Xanthorrhoea* species as having up to eight ovules per carpel.   This means that each fruit has the potential to produce a maximum of 24 seeds.   In reality, the seed number rarely exceeds six, showing an abortion rate of at least 75 per cent of ovules.   As many fruits have been found to produce only one seed, the abortion rate in these cases is 96 per cent, assuming eight ovules were present initially in each carpel. Additional information on abortion of ovules was sought by counting seeds present in each unilocular carpel.   As the plants produced large, columnar, terminal unbranched inflorescences (Pl. XIII) that may reach 4·5 metres in length in *X. resinosa*, it should be possible to see if any correlation exists between high ovule abortion rate and great distance distally from the vegetative axis.   This condition could be expected as the distal tip of the inflorescence is most distant from the food supplied by the vegetative axis.

MATERIALS AND METHODS

Collections of the inflorescences of species of *Xanthorrhoea* were made from the localities listed :

Xanthorrhoea australis R. Br. : Port Welshpool, Victoria—open habitat ; Mt Slide, Victoria—shaded habitat.

X. resinosa Pers. : Top of Bulli Pass, New South Wales—open habitat.

X. preissii Endlich : Perth, Western Australia—open habitat.

RESULTS

Species of the polycarpic woody monocotyledon *Xanthorrhoea* produce ovoid, capsular fruits that are slightly zygomorphic by virtue of a sharp point on the distal end which represents the persistent base of the style and which is situated eccentrically in the mature fruit (Pl. XIII, fig. *b* ; Pl. XIV, fig. *a*).   The fruit's surface is smooth and hard, with three longitudinal furrows opposite the septa of the ovary that alternate with three furrows at the lines of dehiscence (Pl. XIII, fig. *b* ; Pl. XIV, fig. *a*).   They are slightly upturned *in situ*, are about 11 mm long by 5 mm wide and dehisce loculicidally (Pl. XIV, fig. *b*).   As pointed out by Waterhouse (1967) and Lee (1966) the outer three perianth members are rather glumaceous, with terminal tufts of hairs in *X. resinosa* (Pl. XIV, figs *a*, *b*) and are slightly shorter than the petalloid, near-white inner members.

The seeds are shiny, jet black, about 7 mm long by 3 mm broad, with a small white hilum at one end (Pl. XIV, fig. *c*).   They usually have a longitudinal ridge with two sloping sides on one face and a flat third face, being triangular in cross section.   Both Brown (1810) and Bentham (1878) described the embryo as situated in a position transverse to the long axis of the seed but Waterhouse (1967) showed that this position arises as a result of excessive growth in the short axis of the ovules, which he formerly termed amphitropous but are correctly described as hemitropous (Waterhouse, pers. comm. 1974).   Several seeds which did not conform to the general form just described were found to have been

formed in loculi with more than one mature seed present. Plate XIV, fig. *d* shows a pair of seeds that were taken from a single loculus ; the dimorphy is quite evident. Seed length is only 1 mm less in single seeds but the tapered ends are lost in some. Also, an extra transverse ridge is prominent where one seed was pressed against the other in the loculus (Pl. XIV, fig. *d*). Further variations are evident in the rarer instances in which loculi contained three or four seeds, and the seed polymorphism seen is a natural result of crowding within the single loculus. Harper *et al.* (1970) list examples of somatic polymorphism in which seeds differ morphologically on the basis of presence or absence of ornaments such as a pappus or a wing-like bract, on texture or colour in the testa, or on
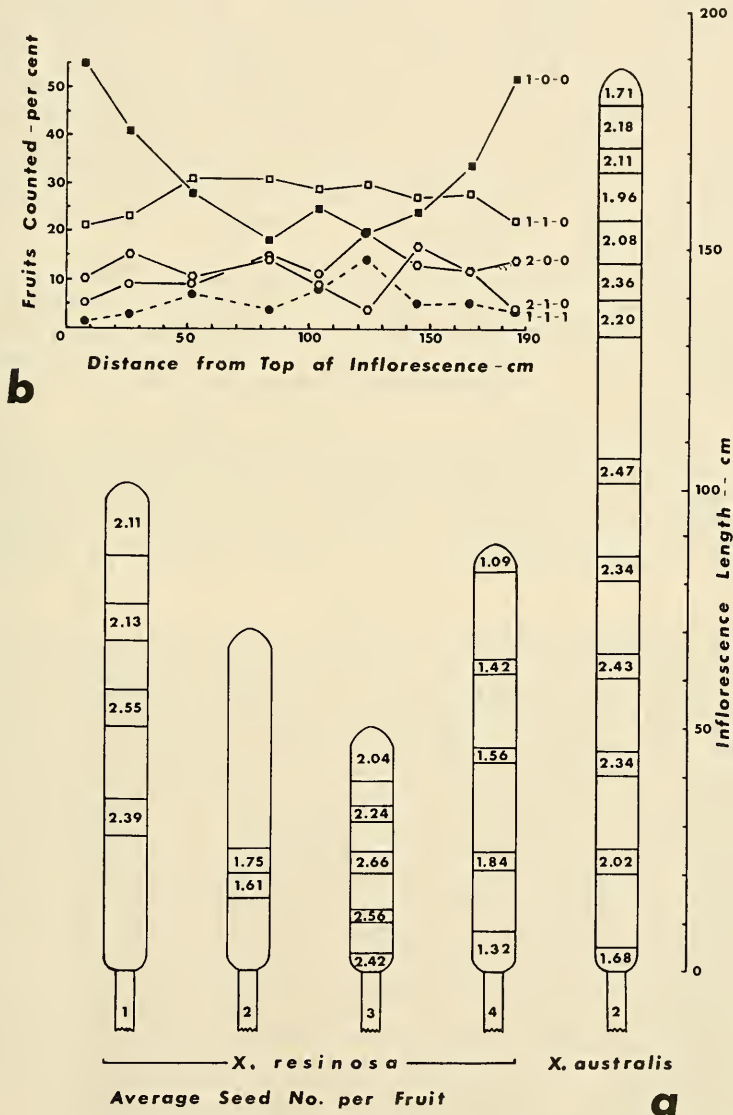

Fig. 1. Fruit productivity in relation to position on the inflorescence axis. a. Relation of average seed numbers in fruits to position on the inflorescence axis. b. Frequency of the most common fruit types with relation to position on the inflorescence axis of *X. australis* in Fig. 1a.

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the basis of size. Although the distinction between singly-occurring seeds of *Xanthorrhoea* and twins is not as marked as in some of the examples of Harper *et al.* (1970), the different forms in themselves are distinct enough to fall within the limits of the term somatic polymorphism.

Table 1 provides data collected from three species of *Xanthorrhoea* which involved the opening and examination of 3,992 fruits and the recording of the positions of just over 10,000 seeds. From the results it is apparent that the fruit types with seed arrangements per loculus (1–0–0) and (1–1–0) are most common, occurring in 34·5 per cent and 30·1 per cent respectively of all the material examined. The next most frequent fruit types were those with seed arrangements (1–1–1) and (2–1–0, 2–0–0 and 2–1–1, in all of which one twin was present), having an overall occurrence in 11·0 per cent, 7·9 per cent, 7·2 per cent and 3·7 per cent respectively of those specimens examined. Other fruit types each contributed to about 1 per cent or less of the specimens examined. Two of the three plants of *X. australis* produced most fruits having multiple seed numbers per loculus, while other specimens had predominantly the combinations of (1–1–1), (1–1–0) and (1–0–0). All possible variations of seed groupings were seen in fruits with from one to four seeds, but above that number possible combinations involving 4, 5, 6, or 7 seeds per loculus were lacking except for one example of (4–1–0).

In the examination of five inflorescences, seed counts of fruits were made at measured intervals along the spikes (Fig. 1*a*). Average seed numbers per fruit were marked on the diagram next to the corresponding part of the inflorescence. It is apparent that seed number per fruit is lowest in an inflorescence at its extremities and higher toward the central part of the inflorescence. This applies even to *X. resinosa* (No. 2), where fruit set was very poor.

A plot of the various fruit types in the inflorescence with most complete data (*X. australis*—No. 2, Fig. 1*b*) reveals no great fluctuations except in fruits with a single seed and two empty carpels. The incidence of these is high at each extremity of the inflorescence and drops off by half in the centre. This accounts for the low seed number per fruit in the extremities of the inflorescence.

Discussion

Before considering abortion rates in the ovules, the method of production of flowers should be briefly stated. Waterhouse (1967) describes the arrangement of floral clusters, which contain from 2 to 11 flowers, depending on the species, as follows : " The sessile flower-clusters in surface aspect have essentially the appearance of juxtaposed parallelograms arranged in helices around the spike ". He states that, in a spike of *X. resinosa*, 11 flower primordia are formed, 6 of which usually abort before anthesis. Allowing for this loss, some 7,500 flowers may still develop in one metre length of inflorescence. If each of these flowers grew to maturity and each ovule (eight maximum per loculus) survived, this would mean a potential of 180,000 seeds per metre length of inflorescence. Although the five surviving flowers per cluster mature at differing rates, providing a mechanism that increases the chances of fruit set by presentation of stigmas over an extended period of time, fruit and seed set is still low. Anthesis is always later at each extremity (10 cm) of an inflorescence than it is in the middle. At each end of an inflorescence there is usually an increase in fruits with only one mature seed (Fig. 1 and Table 1). It thus seems likely that food supply from the vegetative axis is not a factor limiting seed set but rather that the time of anthesis is a more significant controlling factor. With an overall average of 2·1 seeds per fruit of all species examined, it is clear that higher abortion of ovules in late opening flowers is a common phenomenon in these plants. Therefore extension of time of anthesis, although of advantage to the plant if early flowers are harmed in any way, results in high abortion rates of late developers.

Table 1

Fruit fertility in Xanthorrhoea

Seed per fruit	Number per loculus	X. resinosa								X. australis						X. preissii		Totals	Percentages
		1		2		3		4		1		2		3		1			
		I*	II†	I	II	I	II	I	II	I	II	I	II	I	II	I	II		
7	3-3-1	—	—	—	—	—	—	—	—	—	—	2	0·1	—	—	—	—	2	0·1
7	3-2-2	—	—	—	—	—	—	—	—	—	—	2	0·1	—	—	—	—	2	0·1
6	3-3-0	—	—	—	—	—	—	—	—	1	0·1	2	0·1	—	—	—	—	3	0·1
6	3-2-1	—	—	—	—	—	—	—	—	1	0·1	10	0·6	—	—	—	—	11	0·3
6	2-2-2	—	—	—	—	—	—	—	—	3	0·3	8	0·5	—	—	—	—	11	0·3
5	4-1-0	—	—	—	—	—	—	—	—	—	—	1	0·1	—	—	—	—	1	0·0
5	3-2-0	10	1·9	—	—	—	—	—	—	7	0·8	6	0·4	—	—	—	—	23	0·6
5	3-1-1	—	—	—	—	—	—	—	—	1	0·1	6	0·4	—	—	—	—	7	0·2
5	2-2-1	—	—	—	—	—	—	—	—	18	2·0	35	2·1	—	—	—	—	53	1·3
4	4-0-0	—	—	—	—	—	—	—	—	—	—	1	0·1	—	—	—	—	1	0·0
4	3-1-0	—	—	—	—	—	—	—	—	5	0·6	26	1·5	—	—	—	—	31	0·8
4	2-2-0	9	1·7	—	—	—	—	—	—	10	1·1	29	1·7	—	—	—	—	48	1·2
4	2-1-1	25	4·8	—	—	6	2·4	—	—	46	5·1	72	4·2	—	—	—	—	149	3·7
3	3-0-0	—	—	—	—	—	—	—	—	8	0·9	20	1·2	—	—	—	—	28	0·7
3	2-1-0	50	9·6	—	—	2	0·8	—	—	79	8·8	186	10·9	—	—	—	—	317	7·9
3	1-1-1	124	23·8	26	13·0	113	45·2	14	12·6	43	4·8	103	6·1	12	12	4	1·9	439	11·0
2	2-0-0	23	4·4	2	1·0	1	0·4	—	—	72	8·0	189	11·1	—	—	1	0·5	288	7·2
2	1-1-0	206	39·5	82	41·0	100	40·0	39	35·1	259	28·7	436	25·6	46	46	34	16·5	1,202	30·1
1	1-0-0	75	14·4	90	45·0	28	11·2	58	52·3	348	38·6	568	33·4	167	81·1	167	81·1	1,376	34·5
Total		522	100	200	100	250	100	111	100	901	100	1,702	100	100	100	206	100	3,992	100
Average seed number per fruit		2·4		1·7		2·4		1·6		2·0		2·1		1·7		1·2		2·1	

* I = Number of fruits counted with condition in column on far left.

† II = I expressed as a percentage of total fruits counted for that plant.

Actual seed output for the specimens of *X. resinosa* counted in Fig. 1 ranged from a low of 336 in a plant with high floral abortion (No. 2) to a high of about 2,600 in a plant (No. 1) with high floral success. When an adjustment is made for length of spike (relative to data for 1 metre above), these two figures represent $0 \cdot 1$ per cent and $1 \cdot 4$ per cent seed productivity of the maximum potential seed output. When the estimated seed production of 7,500 for the single specimen of *X. australis* is adjusted for a possible maximum of four developed flowers per cluster (instead of the five in *X. resinosa*) and for spike length, a higher seed productivity of $5 \cdot 2$ per cent of the maximum possible is found.

Tomlinson (In press) described a comparable situation of high floral productivity but low seed set in *Corypha elata*. The monocarpic palm produced in the order of ten million flowers but only 250,000 seeds. As each tricarpellary ovary usually produces only a single seed from its three ovules, this means a seed productivity of $0 \cdot 8$ per cent of the maximum potential seed output and again a huge loss of potential seeds by floral and ovular abortions.

Several major points may be made from these results. The abortion rate of ovules from a maximum possible of 24 per fruit reduces final seed number most frequently to two ($37 \cdot 3$ per cent) followed by one ($34 \cdot 5$ per cent), three ($19 \cdot 6$ per cent) and four ($5 \cdot 7$ per cent). The highest success of ovules in a single loculus was four, although only five seeds were produced by that fruit. The maximum number of seeds in a fruit was seven–(3–3–1) and (3–2–2). Somatic seed polymorphism results from crowding of more than one developing seed in a loculus. The most frequent polymorphism resulted from twinning and the incidence of fruits with one set of twins as their only polymorphic seeds accounted for $18 \cdot 8$ per cent of the total counts made, the remainder of fruits with polymorphic seeds being found only in $5 \cdot 7$ per cent of all counts made. According to Harper *et al.* (1970) somatic polymorphism is determined not by genetic segregation but by the internal (or external) environment of the maternal parent. The different morphs may also have different ecological roles, dormancies, weights and dispersal mechanisms. In *Xanthorrhoea*, seeds in pairs are generally smaller than single seeds and this leads one to suggest that different dispersal rates in wind would apply between the larger and smaller seeds. Greatest abortion rates of ovules as evidenced by a high frequency of (1–0–0) fruits occurred at both ends of inflorescences, a situation somewhat similar to abortion of ovules in pea fruits (Linck, 1961).

A comparison of these results with those of other workers can only be limited because of the small sample of plants examined. However, some comments will be made with regard to differences seen as a result of habitat, frequency of flowering and predation. All specimens of *X. resinosa* examined were growing in an open habitat with very little shading and were subject to frequent burning in the dry summer months. This leads to flowering annually as fire stimulates this process in these plants. The specimens of *X. preissii* and the first and third specimens of *X. australis* were growing in a similar habitat but were not subject to frequent burning. Finally, the second specimen of *X. australis* was growing in a shaded area as an understory plant in a dry sclerophyll *Eucalyptus* forest and was one of a group of plants studied (Staff, 1975) in which a maximum rapid growth rate of inflorescence of 49 cm over seven days was recorded, and a maximum length of inflorescence of 300 cm was estimated to have reached that length in 75 days—an overall average elongation rate of 4 cm per day. This plant also had not been subjected to burning for several years and was one of a group that flowers infrequently (inflorescences were not produced by this stand in the four years following the measurement of growth rates).

It appears likely that, on an individual plant basis, total seed output of the more frequently flowering *X. resinosa* plants in an open habitat is less than seed output in the unburnt, shaded *X. australis* plants. If, however, the infrequency

of flowering of the latter plants is taken into consideration, this apparent surfeit of seeds may not necessarily apply in the long term. More measurements are needed to quantify this relation properly.

Limited seed predation has been observed in *X. australis*. The small moth *Hylaletris latro* Zell reproduces on inflorescences of this species and Britton *et al.* (1970) state that the larvae tunnel in the flower spikes. I have observed young larvae inside fruits and older larvae living in the spikes. Evidence of damage of seeds was seen but it was not extensive. The escape of seeds from predators by release from the dehiscing capsules, a mechanism aiding survival against heavy predation by insects in legumes (Janzen, 1969), must apply here, although seeds may be entrapped in open fruits for several months.

Differences in abortion of ovules as evidenced by average seed number per fruits showed no discernable trends but the plants that possessed most poly-morphic seeds in the form of twins, triplets and quadruplets were the *X. australis* inflorescences. This phenomenon could be a reflection of genetical differences between species, or a reflection of greater success of ovules in a physically long structure, or a reflection of the greater size and therefore energy storage capacity of the vegetative stems of *X. australis*, which were the only specimens examined with arborescent stems. Williams and Attwood (1971) and Tripathi and Harper (1973) found that low seed production in perennial monocots such as *Agropyron repens* could be caused by the allocation of considerable energy towards vegetative reproduction in the form of rhizomes that are good food storage organs. So, too, could the infrequently flowering arborescent plants of *X. australis*, which store large amounts of starch in their stems in non-flowering years, then be able to summon vast food reserves when the sexually reproductive event occurs, producing consequently a higher average seed output than the non-arborescent plants. Finally, high abortion rates of ovules could be a reflection of high water stress prevailing at the times of inflorescence initiation and development. In the oil palm, *Elaeis guineensis* Jacq., Hartley (1969) states that, although little is known about abortion of inflorescences, both he and Broekmans (1957) have found some correlations between particularly dry seasons, inflorescence abortions, retarded inflorescence growth and minimum yields of fruits. Meteorological data on rainfall that occurred prior to and during the period of flowering of the *X. australis* plant with high seed polymorphism (No. 2) (Staff, 1975) suggest no dearth of water in that specimen. Unfortunately comparable data are not available for the other specimens examined but it seems reasonable to expect a greater chance of water stress in plants growing in open habitats than in those in shaded areas.

In conclusion it has been shown that seed output in species of *Xanthorrhoea* is well below the possible maximum. Abortion of flowers and ovules is thus very high and the average seed number per fruit is $2 \cdot 1$, although seven seeds have been found in one fruit. Twinning is the most frequent polymorphism, quadruplets were the highest multiple seeds produced. Abortion rates are highest at each end of the inflorescence and reflect the late opening of flowers in these positions. This condition differs from that initially predicted on the basis of the possible limiting effect of nutritional supplies to the distal end of the inflorescence. High abortion rates could be particularly aggravated by water stress in dry open habitats. Frequent flowering tends to produce fewer seeds in the short term but more seeds in the long term. Insect predation is not thought to be a big factor in seed output reduction.

The mechanism in the polycarpic *Xanthorrhoea* of staggered times of anthesis in combination with the production of excessive numbers of flower primordia and high ovular abortions provides a dynamically fluid reproductive stratagem similar to that in the monocarpic palm *Corypha elata*. Its effect is to overcome problems such as intermittent water stresses and insect predations while still providing the plant with an adequate number of disseminules for survival.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

PLATE XIII

Figs a–c. Inflorescences of two species of *Xanthorrhoea*. a,b. *X. resinosa* with maturing fruits about two weeks before dehiscence. Length of inflorescence in the centre=2·2 m. c. *X. australis* after dehiscence of the capsules.

PLATE XIV

Figs a–b. Fruits of *X. resinosa*. a. Immature fruit with perianth members still attached. b. Open capsule with one wall removed, exposing seeds.

Figs c–d. Seeds of *X. resinosa*. c. Solitary seed from a single loculus. d. Twinned seeds from a single loculus.